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2019-11-15

Rissanen , K , Martin-Guay , M-O , Riopel-Bouvier , A-S & Paquette , A 2019 , ' Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy ' , Agricultural and Forest Meteorology , vol. 278 , 107655 . https://doi.org/10.1016/j.agrformet.2019

http://hdl.handle.net/10138/308557
https://doi.org/10.1016/j.agrformet.2019.107655

Agricultural and Forest Meteorology 278 (2019) 107655

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy

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ARTICLE INFO

Keywords:
Biodiversity
Ecosystem functioning
Functional diversity
Canopy structure
Light interception
UAV
Photogrammetry

ABSTRACT

Biodiversity affects ecosystem functioning in forests by, for example, enhancing growth and altering the forest structure towards greater complexity with cascading effects on other processes and trophic levels. Complexity in forest canopy could enhance light interception and form a link between diversity and productivity in polyculture forests, but the effect of canopy structure on light interception is rarely directly measured.

We modelled the canopy surface structure of a tree diversity experiment by photographing it using unmanned aerial vehicle (UAV) and combining the photos into a digital elevation model with photogrammetry tools. We analysed the effects of tree diversity and functional diversity on canopy structural complexity and light interception with a structural equation model.

Our results show that: a) increased structural complexity of the canopy reduces light interception, whereas b) tree diversity increases the structural complexity of the canopy, and has a dual impact on light interception. Tree diversity decreased light interception through the structural complexity of the canopy but increased it probably through canopy packing and crown complementarity. However, the effects of both tree diversity and structural complexity of canopy were smaller than the effect of the functional identities of the tree species, especially the differences between deciduous and evergreen trees.

We conclude that more complexity in canopy structure can be gained through increased tree diversity, but complex canopy structure does not increase light interception in young forests.

1. Introduction

Studies on biodiversity and ecosystem functioning (BEF) in forests have shown that forests with diverse tree species are often more efficient in providing ecosystem services than monocultures. Polyculture forests can be more resilient to changes in environment (Morin et al., 2014; Pretzsch, 2014) and provide more habitats for other organisms, such as berries and game animals (Gamfeldt et al., 2013). They can also have higher productivity and capacity to store carbon in biomass (Paquette and Messier, 2011; Vilà et al., 2013; Ruiz-Benito et al., 2014), which was lately confirmed in a large worldwide analysis (Liang et al., 2016). In addition to observational studies, tree diversity experiments have recently enabled studies on the effects of tree species richness and functional diversity on ecosystem functioning in forests (Bruelheide et al., 2014; Tobner et al., 2014; Paquette et al., 2018). Functional diversity describes the similarities and differences between the functional identities, e.g. leaf longevity or shade tolerance, among species in a community (Laliberte and Legendre, 2010). Tree diversity experiments have shown that, for example, the presence of species with certain functional identities (Tobner et al., 2016) and functional diversity or species richness (Grossman et al., 2017) can increase productivity in young tree communities and that spatial crown complementarity in polycultures can increase light interception and thus, productivity (Williams et al., 2017).

In conclusion, tree diversity and functional diversity are involved in many forest processes, and most of the above ground processes are related to the structural complexity of canopy and canopy surface. The role of canopy in light interception is self-explanatory, but the structure of canopy surface also affects, for example, turbulences and fluxes of water and energy between trees and atmosphere (Parker and Russ, 2004). Tree diversity impacts the structural complexity of canopy (Ishii et al., 2004; Castro-Izaguirre et al., 2016). On one hand, tree species

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https://doi.org/10.1016/j.agrformet.2019.107655
Received 27 July 2018; Received in revised form 3 June 2019; Accepted 7 July 2019

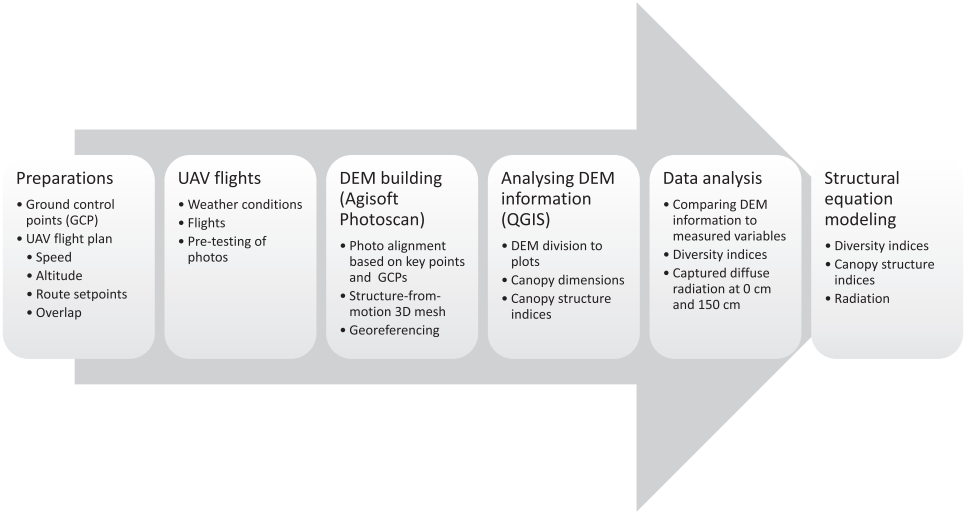

Fig. 1. Workflow. UAV flight, photogrammetry and data-analysis workflow.

with different functional identities, especially related to light use, have different canopy architectures and growth rates (Pretzsch and Schütze, 2005), which leads to greater structural complexity in polyculture forests. On the other hand, in polycultures the plasticity of growth, spatial partitioning of canopy and reduced intraspecific competition can enhance canopy packing (Parker and Russ, 2004; Pretzsch, 2014; Zhang and Chen, 2015; Williams et al., 2017) and thus decrease structural complexity. In addition, canopy structure and complexity affect the availability of habitats (Ishii et al., 2004).

As mentioned above, the structural complexity of forest canopy plays an important role in the distribution and interception of light within the canopy (Jucker et al., 2014; Zhang and Chen, 2015). Structural complexity may increase total leaf area due to canopy stratification or packing and elongation of tree crowns especially near gap areas (Sapijanskas et al., 2014), and leaf area regulates light interception (Parker and Russ, 2004; Pretzsch, 2014; Zhang and Chen, 2015). For example, mixing shade-tolerant and shade-intolerant species can further enhance light interception (Canham et al., 1994; Niinemets, 2010). In turn, light interception influences both tree growth and productivity, as well as the light environment on the forest floor (and related processes, such as, succession). All in all, the structural complexity of forest canopy and possibly enhanced light interception could explain part of the enhanced productivity in polycultures in comparison to monocultures (Hardiman et al., 2013; Jucker et al., 2014; Williams et al., 2017). However, some studies also show nonsignificant or negative connections between tree diversity and canopy structural complexity (Hardiman et al., 2011), leaf area, canopy structural complexity and productivity (Long and Shaw, 2010; Soares et al., 2016), or light interception and productivity (Ryan et al., 2010).

Although light interception is a major element in explaining forest productivity, the processes leading to enhanced light interception in polycultures are not thoroughly understood. The combined effects of tree diversity, species' functional identity and structural complexity of canopy on light interception have been addresses only in few studies. For acquiring a good understanding on the canopy dimensions and structural complexity, 3D modelling techniques based on photogrammetry are a cost-effective option. This field has developed considerably, enabling low-cost 3D modelling of diverse objects and landscapes with a consumer camera (Anderson and Gaston, 2013; Nex and Remondino, 2014). In forests, these modelling techniques are nowadays widely used and serve, for example, in monitoring forest structure and recovery by measuring canopy openness and roughness (Kattenborn et al., 2014; Zahawi et al., 2015) and canopy dimensions by measuring stand height, volume and aboveground biomass (Dandois and Ellis, 2010, 2013; Zahawi et al., 2015).

Our aims were to use UAV-based photogrammetry methods for obtaining information on the canopy dimensions and structure of experimental tree communities, in order to shed new light on the links between tree diversity, canopy structural complexity and the capacity of the canopy to intercept light. Our hypotheses were:

1) the structural complexity of canopy is a function of tree species diversity or their functional diversity and functional traits, and
2) the share of radiation captured by canopy is a function of tree diversity and the structural complexity of the canopy.

2. Methods

2.1. Location

We studied the hypotheses on a biodiversity experiment located on the Macdonald Research Farm at McGill University (Sainte-Anne-de-Bellevue, Quebec, Canada, 45°28′ N, 73°45′ W, 36 m a.s.l.). The experiment, part of IDENT (Tobner et al., 2014) and TreeDivNet (Paquette et al., 2018) was established in the spring of 2009 on former agricultural land, comprising almost 15 000 trees. Trees stand in 216 Cartesian grid plots containing 64 densely planted individuals (8 × 8 rows; 50-cm spacing). Plots are separated from each other by ˜1.25 m corridors. Tree species include 12 North-American and 7 European evergreen and deciduous species in monocultures and polycultures of 2, 4 or 12 species. The species mixtures allow separating the effects of species richness (SR) and functional diversity (FD). The mixtures are replicated in four blocks. For further details and species listing, see Supplementary material Table S1, Tobner et al. (2014, 2016) and Verheyen et al. (2016). The site is flat, but a precise micro-topography digital elevation model of the ground surface has been measured using a total station theodolite to account for minor depressions and bumps.

2.2. Digital elevation model (DEM)

2.2.1. UAV flights

The workflow from UAV flight planning to data-analysis is presented in Fig. 1. To build digital elevation model (DEM) of canopy surface, we took a series of aerial photos of the experiment by UAV (unmanned aerial vehicle) platform model DJI Innovations S800, provided and operated by EXO Tactik Air Support. The flights took place on 28th of July 2015. Prior to the flights, we established twelve locally and globally georeferenced ground control points (GCPs) around the

experiment and calculated the flight plan including speed, altitude and route set points (Supplementary material Fig. S1). The distance between each leg of the flight pattern was adjusted to the resolution and focal length of the camera, as well as to the UAV altitude, to ensure a 70% side overlap of the photos. The flying speed of the UAV was synchronised with the photo frequency (1 photo per second) for a 90% frontal overlap of the photos. Flying altitude from the ground was 50 m, on average 45 m from the canopy surface. The sampling distance was 3.0 cm/pixel at ground level, and at the canopy surface approximately 2.7 cm/pixel. The camera was an off-the-shelf consumer camera GoPro HERO3 + Black Edition (GoPro, California, United States) with a focal length of 2.77 mm and a built-in GPS for geotagging each photo. It was installed under the platform so that the field of view pointed directly downwards and was free from foreign objects.

After flights, we pre-tested the photos to ensure an optimal quality (sharp photos with sufficient overlap and without foreign objects) and accuracy of DEM. In photogrammetry, uniform positioning and lighting of the studied subject is important. Optimal conditions for the data collection flights are either when the sky is clear of clouds or completely overcast. Cloud overcast provides even lighting conditions throughout the site, thus minimizing sharp shadows and offering better photo exposition of the whole canopy structure. During our flights, the sky was generally cloudy, but not completely overcast. We suggest that during clear days, flights should be set during zenith hours to minimize shadows on the lower leaves and treetops of the canopy, during overcast days this is less important. Our flights took place between 11 and 13 o'clock. Low wind conditions are necessary to prevent leaves and treetops from moving between photographs. The wind speed during our flights was 7–10 km/h, and 10 km/h could be considered the maximum wind speed for good quality images.

2.2.2. Photogrammetry

We used the computer vision software Agisoft PhotoScan Professional edition (version 1.2.1. 2015 Agisoft LLC, St. Petersburg, Russia) for the photogrammetry procedure and DEM building. We did no image processing for the GoPro photos prior to using the software. The software automatically aligned the photos based on their GPS tags and similar features (key point matches). Then, based on structure-from-motion process the software built a point cloud and 3D polygon mesh of the area covered by the photos. The 3D polygon mesh could be covered with orthomosaic that is a planar mosaic of the original photos retaining the original colours (Fig.2). Based on the 3D polygon mesh, the software also created a raster form DEM (Supplementary material Fig. S2). DEM can be georeferenced based on the known GCPs coordinates, but we used the only DEM within the local coordinates of the experiment. For more information on the computer vision structure-from-motion process, see Verhoeven (2011) and Nex and Remondino (2014).

We further analysed the raster form DEM with open source geographic information system QGIS (version 2.10.1-Pisa). Prior to analysis, we reduced the plot size from 8 × 8 trees to 6 × 6 to reduce possible bias from the outermost trees (growing in proximity to other treatment plots). Then, based on the DEM of canopy built by PhotoScan

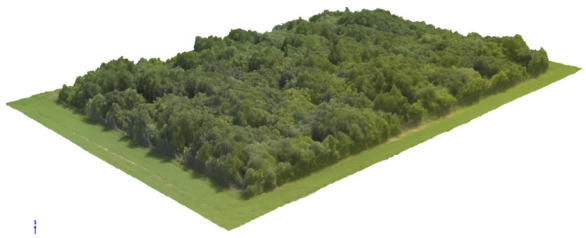

Fig. 2. Digital elevation model of the experiment (DEM). The 3D mesh of digital elevation model with orthomosaic colors generated for the tree diversity experiment, created with Agisoft PhotoScan.

(pixel size 0.05 m) and DEM of ground (pixel size 0.10 m), we calculated minimum, maximum and mean values of plot tree height, as well as height variance for each plot by SAGA library tools (Conrad et al., 2015) to test the DEM quality by comparing with corresponding measured values. Furthermore, to describe the structural complexity of the canopy, we calculated three different surface structure indices for each plot: the ratio of 3D surface to 2D surface, canopy roughness (largest difference between a pixel and surrounding pixels) and TRI (terrain ruggedness index, mean difference between a pixel and surrounding pixels). For the last two we used QGIS GDAL tools (Wilson et al., 2007). Since all three indices correlated strongly, we used only roughness to describe canopy structural complexity in further analysis.

2.3. Light and tree data measurements

Tree size data, including tree height and diameter at 5 cm from the ground, are measured annually at the experiment site. The heights used in this study were measured in spring 2015 and diameters in fall 2015, including only living trees. Diffuse radiation was measured between July 28th and August 7th of 2015 inside each plot in five different locations and two levels: ground level (0 cm) and 150 cm (inside the canopy) from ground by BF Sunshine sensors (Delta-T Devices; models 2, 3 and 5). We used the method described in Paquette et al. (2007) to separate the diffuse component of incoming light from the highly variable direct component that cannot be used to estimate average light availability. Reference radiation was measured in an open field next to the experiment.

We calculated the average seasonal available light inside the plots by dividing the diffuse radiation in the plot by the reference open diffuse radiation value (Paquette et al., 2007). In the few cases where this value was larger than one, i.e. more light was detected under canopy than on open field due to sensor precision, it was corrected to one. Then, we normalised the values by transforming the absolute zero and one values following Smithson and Verkuilen (2006) $y' = (y \times (N - 1) + 0.5) / N$, where y is the transformed value and N sample size and applying logit transformation. Finally, we calculated the mean share of available light for each plot and measurement height and inversed the values to represent the mean radiation captured by the canopy, hereafter called light interception.

2.4. Data analysis

To analyse the quality of the DEM, we compared the DEM-derived height values (modelled height) to the measured plot mean tree height, and the DEM-derived variance (modelled variance) to the measured tree height variance. Measured values were based first on all the trees of the plot, and then only on the dominant trees (taller than 65% percentile of height) because mainly the dominant trees can be captured from an aerial photo. Measured tree height variance was also used as a variable for the canopy structural complexity and it also served as a measured counterpart for the DEM derived roughness.

To describe the tree species diversity of the experiment plots, later referred to as tree diversity, we calculated Simpson's index, FD (functional diversity), FDis (functional dispersion) and Shannon's index (1D) for each plot. The indices were weighted by the basal area of each species on the plot, excluding the outermost trees to avoid possible border effects. 1D proved to be the most efficient predictor for roughness and light interception, therefore it was used as the variable describing tree diversity in further analysis. Furthermore, we used an index of functional identity – the community weighted mean of leaf longevity (CWM Llo) - to represent the structural and optical differences between evergreen and deciduous trees and their combinations. Larger values of CWM Llo indicate a larger proportion of plot canopy consisting of long-living (evergreen) needles. Prior to any analysis, roughness, tree height variance, 1D and CWM Llo were log-transformed for normality.

For analysing the tree diversity effects on the structural complexity of the canopy (described by canopy roughness and measured tree height variance) and light interception, we calculated net effect of tree diversity (NE) and proportional deviation (D_T) for each polyculture plot. NE for a polyculture plot is calculated from the difference between the observed value for a certain variable and its expected value. This expected value is based on the observed values of corresponding monocultures within the same block and is weighted by stem volumes of each species in the polyculture plot (Loreau, 1998). D_T is the relative version of NE and results from the division of NE by the expected value (Loreau, 1998). Because D_T did not add new information to NE, in further analysis we only used NE. We tested each NE against test value 0 in one-sample Student *t*-test and analysed their relations to species richness (SR) by multiple comparison between SR classes. We also calculated Pearson's correlations (r) between the variables over all the plots. The analyses touched all the plot types (N = 216 for correlation analysis or N = 140 for NE analysis that include only polycultures), and the different plot types separately: pure evergreen (n = 72 or 36), pure deciduous (n = 60 or 20), and mixed plots (n = 84 in both analysis) including both evergreen and deciduous trees.

To build a more comprehensive picture of the linkages between tree diversity, the structural complexity of canopy and light interception, along with the effects of other parameters such as stand dimensions, we built a structural equation model (SEM). SEM allowed to separate the confounding effects of different parameters, and to better understand the possible interrelation between explaining parameters. We ran the model with different plausible parameter combinations and chose the best parameter and interaction combination with the following criteria: 1) all the pathways are significant ($p < 0.05$), 2) the whole model Chi-square test is not significant ($p > 0.05$), 3) Tucker-Lewis and Comparative Fit indices are close to 1, and 4) the coefficients of determination (R^2) for the captured light and roughness are meaningful (over 0.20). These criteria supported each other so that we did not need to compromise between them when choosing the final model. The exogenous parameters of the final model were: 1D and CWM Llo and explained parameters: measured total basal area and mean height of the plot trees, DEM derived roughness, light interception at ground level (0 cm) and inside the canopy (at 150 cm). As a measurement-based option for canopy roughness, we also added measured tree height variance in order to compare the effectiveness of modelled and measured parameters that describe the structural complexity of the canopy.

For the numerical analyses, we used both R version 3.3.1 (The R Foundation for Statistical Computing), packages FD (Laliberte and Legendre, 2010), vegan (Oksanen et al., 2013) and lavaan (Rosseel, 2012), and Matlab version R2015a (The Mathworks, Inc., Natick, Massachusetts, United States).

3. Results

3.1. DEM performance

The DEM that was built based on UAV aerial photos had a high resolution (point density 417 points/m^2 and resolution 0.05 m/pixel) and its accuracy was on average 0.1 m horizontally and 0.07 m vertically, compared to the georeferenced ground control points (GCPs). The DEM model estimated well the plot mean tree height of dominant trees that are visible from above (taller than 65% percentile) ($r = 0.93$, $p < 0.01$, RMSE = 0.436)). When all the trees, even the small trees completely hidden by the dominant canopy were included, the estimation was not as good ($r = 0.65$, $p < 0.05$, RMSE = 0.928) (Fig. 3).

The DEM derived canopy height variance that covers the variance over the whole surface of the canopy did not correspond to the measured height variance of all trees ($r = 0.11$) or even the dominant trees ($r = -0.12$), over all the plots (Fig. 4). In evergreen plots the relation between measured variance of the dominant trees and modelled variance was even negative ($r = -0.27$, $p < 0.05$) (Fig. 4). The same

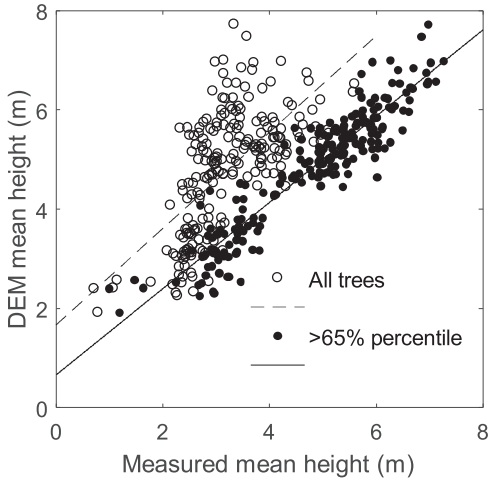

Fig. 3. Tree height estimate from digital elevation model (DEM). DEM modeled plot mean tree height and measured plot mean height of all trees of plots (open dots) $r = 0.65$ ($p < 0.05$) or dominant trees, meaning trees taller than 65% percentile (full dots) $r = 0.93$ ($p < 0.01$). Includes all the plots (N = 216).

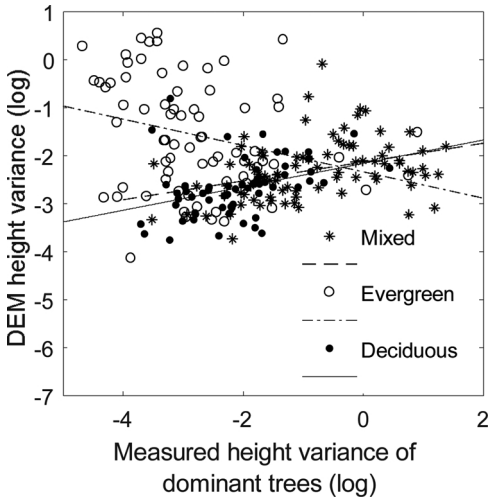

Fig. 4. Tree height variance estimate of the digital elevation model (DEM). The relations between DEM derived roughness (log transformed) and measured mean tree height variance of dominant trees (log transformed) per plot. All plots $r = (-0.12)$, mixed $r = 0.36$ ($p < 0.01$), evergreen $r = -0.27$ ($p < 0.05$), deciduous $r = 0.35$ ($p < 0.01$). Includes all the plots (N = 216).

applied to the DEM derived canopy roughness and measured tree height variance. Including also the understorey trees, the correlation between the two variables used to describe the structural complexity of canopy was -0.37 ($p < 0.001$), in evergreen plots -0.40, ($p < 0.01$), but positive in deciduous plots ($r = 0.33$, $p < 0.05$).

3.2. Tree diversity effects on the structural complexity of canopy

The differences between the canopy roughness of monoculture and polyculture plots (Table 1) were not significant, along with the correlation between roughness and tree diversity (1D). On the contrary, tree height variance was significantly higher in polyculture plots compared to monocultures (Table 1).

However, the net effect (NE) of tree diversity on canopy roughness was significantly different from zero over all the plots, as well as in the deciduous and mixed plots (Table 2). The NE of tree diversity on tree height variance was significant in all the plot types (Table 2). Significant NE indicates that the structural complexity of canopy exceeded the complexity that could be expected from monoculture values, thus, a

Table 1
Variables used in the analysis and their mean values in different plot types: monocultures and polycultures, as well as deciduous, evergreen and mixed. Variable's mean values differ significantly (multiple comparison with Tukey HDS correction) between mono- and polycultures, or between deciduous, evergreen and mixed stands, where different letters are printed (only where the effect was significant).

Average:	SR	1D	CWM Llo	Roughness	Measured height variance	Measured mean height (m)	Total basal area (m^2)	Light interception 0 cm	Light interception 150 cm
All plots (N = 216)	2.87	0.6	2.6 (0.87)	−1.4 (0.31)	0.4 (1.14)	3.2 (0.82)	0.111 (0.028)	6.4 (1.98)	4.8 (1.66)
Monocultures (n = 76)	1.0	0.0	2.7 (1.11)	−1.5 (0.41)	−0.4 a (1.10)	3.3 (1.08)	0.114 (0.033)	6.4 (2.13)	4.6 (1.93)
Polycultures (n = 140)	3.9	0.9	2.58 (0.70)	−1.4 (0.24)	0.7 b (0.94)	3.2 (0.63)	0.107 (0.024)	6.5 (1.90)	4.8 (1.50)
Deciduous (n = 60)	1.7 a	0.3 a	1.7 a (0.06)	−1.6 a (0.18)	0.7 a (0.45)	4.2 a (0.57)	0.118 a (0.027)	4.9 a (1.28)	4.7 (1.10)
Evergreen (n = 72)	1.9 a	0.4 a	3.4 b (0.64)	−1.3 b (0.40)	−0.8 b (1.02)	2.6 b (0.55)	0.106 b (0.029)	7.7 b (1.73)	5.1 (2.31)
Mixed (n = 84)	4.6 b	0.9 b	2.5 c (0.53)	−1.5 c (0.21)	1.1 c (0.62)	3.1 c (0.48)	0.113 (0.025)	6.1 c (1.76)	4.6 (1.27)

Note: Standard deviation between parenthesis. SR = species richness, 1D = Shannon's index, CWM Llo = Community weighted mean of leaf longevity. 1D, roughness, measured height variance and CWM Llo were log transformed, and light interceptions at 0 cm and 150 cm logit transformed.

Table 2
Mean NE one sample *t*-tests (against test value 0) on roughness and tree height variance of plot types. Bold values are significant at 95% confidence level, p-values of the *t*-test in parentheses.

Polyculture plots	Roughness	Tree height variance	Light interception 0 cm	Light interception 150 cm
All (N = 140)	**0.13** (< 0.001)	**0.69** (< 0.001)	**0.845** (< 0.001)	0.07 (0.50)
Deciduous (n = 20)	**0.13** (0.01)	**0.32** (0.01)	0.246 (0.31)	0.28 (0.20)
Mixed (n = 84)	**0.17** (< 0.001)	**0.83** (< 0.001)	**1.110** (< 0.001)	0.02 (0.99)
Evergreen (n = 36)	0.04 (0.50)	**0.5** (< 0.001)	**0.558** (0.02)	0.13 (0.66)

positive effect of tree diversity. NE on roughness in relation to species richness was not significant, but NE on tree height variance increased from plots with two species to plots with four species over all the plots and in mixed plots (Supplementary material Fig. S3).

Both tree height variance and roughness differed significantly between plot types (pure evergreen, pure deciduous and mixed plots) (Table 1). They were largest in evergreen, especially spruce plots and smallest in deciduous plots (Table 1), corresponding to the positive correlation found between roughness and community weighted mean of leaf longevity (CWM Llo) that describes the structural and functional differences between evergreen and deciduous species (Fig. 5). In addition, canopy roughness correlated negatively with plot basal area ($r = -0.48$, $p < 0.01$) and mean height ($r = -0.55$, $p < 0.01$) over all the plots, but especially in evergreen plots ($r = -0.71$, $p < 0.01$ and $r = -0.62$, $p < 0.01$ respectively).

3.3. Effects of tree diversity and structural complexity of canopy on light interception

Light interception at ground level (0 cm) or inside the canopy (at 150 cm) did not differ between monoculture and polyculture plots (Table 1), and only correlated with tree diversity (1D) significantly yet weakly in evergreen plots at ground level ($r = 0.22$, $p < 0.05$). The NE on light interception was significantly different from zero at ground level, but insignificant at 150 cm (Table 2). However, in deciduous plots, the effect was not significant even at ground level, and in evergreen plots the effect was weak (Table 2). At ground level, NE on light interception increased significantly from plots with two species to plots with four species over all the plots and in mixed plots (Supplementary material Fig. S4).

The variables describing the structural complexity of canopy - roughness and tree height variance - had negative correlations with light interception over all the plots, but not separately in deciduous plots (Fig. 6). Measured tree height variance correlated negatively with light interception at ground level and canopy roughness inside the canopy (Fig. 6).

At both measurement levels, light interception was smallest in deciduous plots and largest in evergreen plots, but the differences between plot types were significant only at ground level (0 cm) (Table 1). Correspondingly, at ground level, the correlation between light

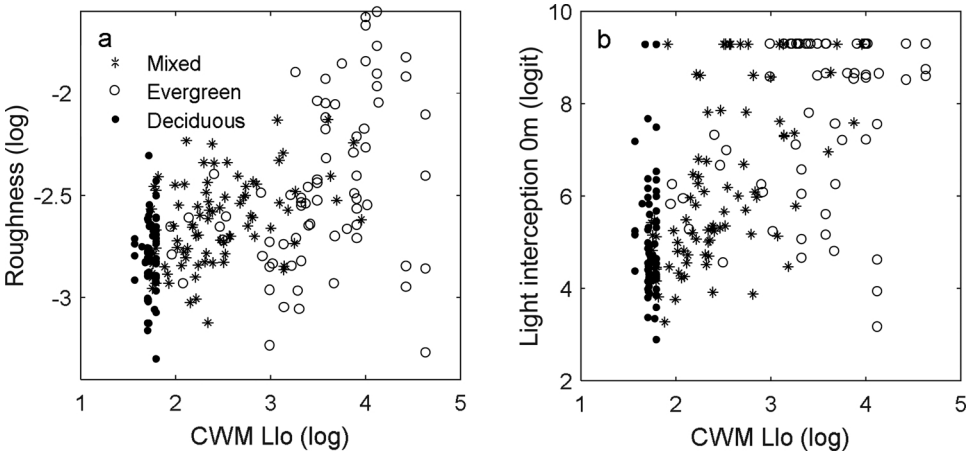

Fig. 5. Effects of functional identity on structural complexity of canopy and light interception. The relations between community weighted mean of leaf longevity (CWM Llo, log transformed) and a) DEM derived roughness (log transformed), all plots $r = 0.53$ ($p < 0.01$), mixed plots $r = 0.42$ ($p < 0.01$), evergreen plots $r = 0.38$ ($p < 0.01$), deciduous plots $r = (-0.10)$ and b) light interception at ground level (logit transformed), all plots $r = 0.66$ ($p < 0.01$), mixed plots $r = 0.56$ ($p < 0.01$), evergreen plots $r = 0.32$ ($p < 0.01$), deciduous plots $r = (-0.10)$. Includes all the plots (N = 216).

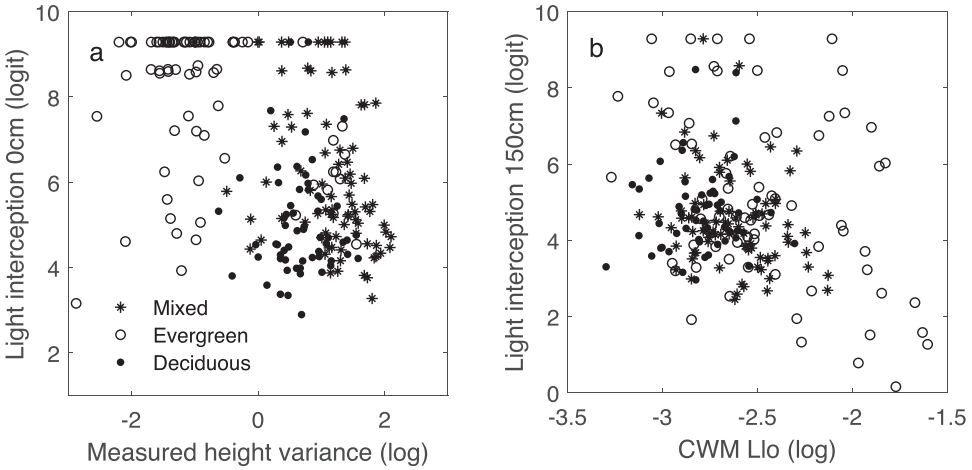

Fig. 6. Effects of structural complexity of canopy on light interception. The relations between a) measured height variance (log transformed) and light interception at ground level (logit transformed), all plots $r = -0.50$ ($p < 0.01$), mixed $r = -0.39$ ($p < 0.01$), evergreen r = -0.28 ($p < 0.01$), deciduous r = (0.07) and b) the relations between DEM derived roughness (log transformed) and light interception inside the canopy (logit transformed), all plots r = -0.24 ($p < 0.01$), mixed $r = -0.23$ ($p < 0.05$), evergreen $r = -0.38$ ($p < 0.01$), deciduous r = (0.07). Includes all the plots (N = 216).

interception and CWM Llo was significant over all the plots (Fig. 4). In addition, basal area and plot mean height affected light interception differently in pure evergreen and pure deciduous plots. In evergreen plots the correlations were positive ($r = 0.43$, $p < 0.01$ and $r = 0.56$, $p < 0.01$ respectively), but negative in deciduous plots (r = -0.26, $p < 0.05$ and r = -0.30, $p < 0.05$ respectively). In mixed plots, the correlation between basal area and light interception was negative (r = -0.39, $p < 0.01$).

3.4. Structural equation model

The SEM models combined the effects of tree diversity, described by 1D and tree functional identities, described by CWM Llo on canopy light interception, and these effects were partly mediated through basal area, plot mean height and structural complexity of the canopy described by canopy roughness and measured tree height variance (Fig.7). At ground level, the main effect on light interception was the strong positive effect of CWM Llo (0.75), but canopy roughness had a small negative effect (-0.19) and tree diversity (1D) had a small positive effect (0.10) (Fig. 7). 1D also had a small indirect negative effect on light interception through plot mean height and roughness (the multiplication of successive arrow coefficients: -0.13 x -0.21 x -0.19 = -0.005), and basal area a small indirect positive effect through canopy roughness (0.29 x -0.21 x -0.19 = 0.012) (Fig. 7). The model fit was acceptable based on the evaluators (Fig. 7). It explained roughly half of the variation in diffuse light interception (Fig.7) but failed to estimate times when all light was captured and predicted an excess of cases where very little light was captured (Supplementary material Fig. S5). Inside the canopy (at 150 cm), the model captured poorly the variation in light interception and the only parameter that directly affected light interception was canopy roughness (-0.23) (Supplementary material Fig. S6). Neither of the models indicated a significant effect of height variance on canopy roughness or light interception.

4. Discussion

4.1. DEM performance in estimating canopy dimensions and structure

Based on photographs taken from UAV, we built a digital elevation model (DEM) of the experiment canopy and expected it to capture the canopy's dimensions and surface structure. The DEM represented well the mean height of dominant trees in plots (taller than the 65% percentile of the plot trees) ($R^2 = 0.87$), corresponding to results of Dandois and Ellis (2010, 2013), with R^2 from 0.52 to 0.83. However, because the UAV photogrammetry does not see the understorey trees below the dominant canopy, the DEM does not represent well the mean height over all the trees. This creates a systematic error that needs to be taken into account when estimating the mean height of all the trees on stands with more than one canopy layer. Dandois and Ellis (2010, 2013) also report similar limitation in the technology.

We also observed that DEM derived canopy roughness or height variance describe the canopy structure in a different way than measured tree height variance. Measured tree height variance takes into account only the tallest points of the trees, whereas DEM derived variables describe the whole visible canopy surface structure of the tree. This was especially pronounced on the evergreen plots because with their typically strong apical dominance and a cone-shaped, bottom heavy crown, young evergreen trees of the experiment (spruces, firs and

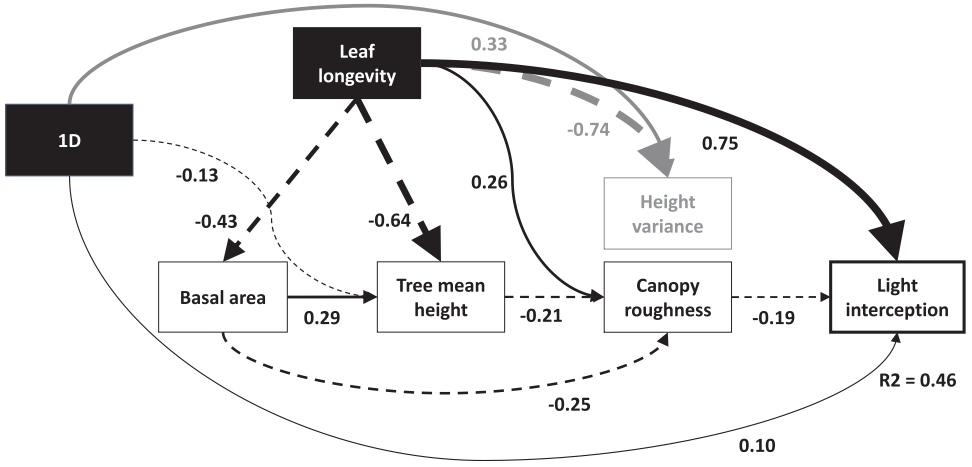

Fig. 7. Structural equation model (SEM). SEM for diffuse radiation at ground level (0 cm). Solid arrows show a positive effect and dashed arrows a negative effect. The grey arrows show effects that do not affect the captured light. The coefficient values and the width of the arrows represent the relative weight of the relation. All relations are significant at 95% confidence level. P-value for Chi-square test 0.41, Tucker-Lewis index 0.1, Comparative Fit Index 0.1001, RMSEA 0 and SRMR 0.024.

pines, see Supplementary material Table S1) form a rough canopy that is not described by merely measuring the height of each tree. Because of this, DEM effectively distinguished the different tree structural types.

Overall, we found that UAV photogrammetry-based DEM provided an accurate and useful presentation of the height and structural complexity of the dominant canopy, or the whole canopy on stands with a single canopy layer.

4.2. Structural complexity of canopy in relation to tree diversity

We hypothesised that the structural complexity of the canopy, described with DEM derived canopy roughness is a function of tree diversity. We found that tree diversity generally enhances canopy roughness in polycultures compared to monocultures with same species, which corresponds to earlier studies (Ishii et al., 2004; Castro-Izaguirre et al., 2016). However, the structural equation model indicated that the positive effect of tree diversity on canopy roughness is small and indirect: it is mediated through stand mean height and stand maturity. Tree diversity affects tree mean height negatively, for example, due to changes in the species' growth patterns and stratification, and a lower symmetric and intraspecific competition in monoculture stands than the interspecific competition in polyculture stands (del Río et al., 2016). The negative link from tree mean height to roughness probably reflects relative maturity of a plot. The experiment consists of young but densely planted trees; thus, a tall plot is analogue to tree maturity, and closed, dense canopy without gaps. On the contrary, in mature, late succession forests the structural complexity of canopy increases with age, because the loss of pioneer trees leaves gaps and the development of late-successional species increases canopy variability (Parker and Russ, 2004; Lei et al., 2009; Hardiman et al., 2011).

Although significant at the whole experiment level, as well as in deciduous and mixed plots, the effect of tree diversity on canopy roughness seemed insignificant in evergreen plots. In monocultures, homogenously growing young evergreen trees with low architectural plasticity create a rough surface with deep gaps between elongated tree crowns. When two or more evergreen species mix, the complementarity of their canopy architectures enables more efficient canopy packing (Jucker et al., 2015; Williams et al., 2017). This packing might decrease the roughness and structural complexity of the canopy and counteract the effect of diversity through tree height.

The tree diversity effect on tree height variance was positive and direct, according to SEM and NE analysis. This result is in line with earlier findings: tree height standard deviations increases with increasing diversity (Castro-Izaguirre et al., 2016) as well as the complexity of vertical and horizontal distribution (Ishii et al., 2004). Tree diversity increases variability in tree size due to species' different growth patterns and thus promotes multi-layered canopy. The tree diversity effect can be further enhanced by increasing species richness.

4.3. Effects of tree diversity and structural complexity of canopy on light interception

4.3.1. Structural complexity of canopy and light interception

Our second hypothesis was that tree diversity would increase diffuse light interception through increased structural complexity of canopy. However, we found that parameters describing the structural complexity of the canopy affected light interception negatively, contrary to what has been suggested earlier (Hardiman et al., 2013). Canopy roughness correlated negatively with light interception inside the canopy, because it describes the dominant canopy. This can be seen also in the SEM for light interception at 150 cm, where roughness is the only significant parameter explaining light interception. Tree height variance correlated negatively with light interception at ground level, because it accounts for the effect of understorey trees, too. However, SEM that accounts also for the confounding effect of different structures of trees (CWM Llo) only indicated a negative effect of canopy roughness on light interception and no significant effect of height variance both at ground level and in the canopy. This highlights the importance of the uniformity of the dominant canopy over the effect of understorey trees in light interception and creating the under-canopy light environment.

The negative effect of canopy roughness on light interception indicates that in young stands, a smooth and uniform canopy captures radiation better than a rough canopy, especially if the rough canopy has gaps between the tree crowns. This effect was detected also in mixed plots with a stratified canopy which is often considered efficient in intercepting light (Ishii et al., 2004) although rarely directly measured. Roughness and gaps in the top strata of a mixed plot facilitate light penetration and interception in lower strata cannot compensate for it. Our results correspond to the models of Ligot et al. (2016) showing a slightly lower light interception in structurally heterogeneous stands compared to homogenous stands. However, contrary to evergreen and mixed plots, in deciduous plots, light interception seemed to be independent from canopy roughness.

4.3.2. Tree diversity and light interception

As discussed above in sections 4.2 and 4.3.1, we found that tree diversity generally increases the roughness of canopy, and canopy roughness decreases the light interception of the canopy. This implies an indirect negative effect of tree diversity on canopy light interception. Yet, this effect is small, as indicated by SEM coefficients. We also found that tree diversity has a larger positive effect on the light interception that is independent from canopy roughness. This positive effect is indicated by the SEM and the significant NE on light interception. This result is in line with that of Ligot et al. (2016), showing a positive diversity effect on light interception in polyculture stands. This positive effect of tree diversity is probably mediated through canopy packing and higher leaf area in polycultures compared to monocultures, as well as complementary light-use strategies between species (Jucker et al., 2014, 2015; Williams et al., 2017). The NE on light interception can increase slightly with increasing species richness and especially in mixtures of evergreen and deciduous trees.

In accordance with Tobner et al. (2016) who found that functional identity had great importance for explaining NE on biomass, we found that CWM in leaf longevity was the most important factor explaining light interception. CWM Llo, representing a deciduous-evergreen continuum, affected strongly all the model parameters. It had a strong positive impact on canopy roughness due to the structural differences between evergreen and deciduous tree canopies on the site. On the contrary, its effect on tree height variance was negative, indicating homogenous height growth in evergreen plots in comparison to deciduous plots. CWM Llo also had a significant positive effect on the captured light at ground level (Fig. 4) that was independent from the tree diversity and roughness effects. The CWM Llo effect is probably connected to the fact that most of the evergreen trees on our experiment are shade-tolerant slow-growing species with long-leaved leaves and elongated crowns that can accumulate high leaf area and have a high capacity for light interception (Messier et al., 1998, Niinemets, 2010. Ligot et al., 2016). Likewise, according to Canham et al. (1994), light penetration through the canopies of early-successional species is higher compared to late-successional species. Because of the slower initial growth of evergreens trees in the experiment, the CWM Llo effect on mean height and basal area of the plot is negative.

Our SEM model explained 46% of the variation in light interception at ground level. This result is close to the 37–55% of understorey light explained by a model including stand density, basal area and stand density index of a structurally heterogeneous mature Douglas-fire forest (Lochhead and Comeau, 2012). Inside the canopy, however, the SEM model was unable to explain the variability in light interception. Potentially a meaningful feature affecting the light interception, which was not directly included in the model, is the openness under the canopy. Many of the tall deciduous trees had already shed some lower branches, whereas the evergreens had not. The openness under

deciduous plots might have allowed some light to penetrate from the sides rather than only from above through the canopy, affecting the light interception.

5. Conclusions

We found that UAV photogrammetry tools are useful in describing the height and structural complexity of dominant canopy of young forest and could provide a cost-effective alternative to airborne LiDAR. The UAV photogrammetry-based elevation model and light measurements showed that in young forests, the light interception of the canopy is mainly determined by the functional traits of the trees – stands with evergreen trees were most efficient in capturing light – and less by the structural complexity of the canopy and tree diversity. Tree diversity increases light interception probably due to canopy packing and complementarity of crowns, but also slightly decreases it by increasing the structural complexity of the canopy. We also observed that the structure of the dominant canopy seems to be more important in explaining light interception than the structure of the whole canopy including understorey trees, with smooth dominant canopy generally providing the most efficient light interception.

In conclusion, the positive net effect of tree diversity on light interception could explain some of the increased productivity that has been detected in polyculture forests in comparison to monoculture forests, but the diversity effect depends strongly on the ability of the mixed tree crowns to form a dense, smooth canopy. This study was conducted in a young forest stand, where self-thinning had not yet occurred. Similar studies in later phases of stand development are needed to understand how the effect of tree diversity on canopy structure and light interception changes with time.

Acknowledgements

The study site is part of McGill University and we very much appreciated their support. The authors would also like to thank the field teams on the experiment and Mélanie Desrochers for her generous help with GIS calculations. The research was funded by NSERC Partnership Engage Grants (Canada) and University of Helsinki travel grant for international traineeship (Finland).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2019.107655.

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